

On the Structure of the Spermiducal Glands and Associated Parts in Australian Earthworms. By GEORGINA SWEET, M.Sc., Melbourne University. (Communicated by Prof. G. B. HOWES, Sec. Linn. Soc.)

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(PLATES 14 & 15.)

IN the present somewhat unsatisfactory condition of the classification of the Australian earthworms, additional knowledge on important points in their anatomy is much needed. At the suggestion of Prof. Spencer, the following investigation has been carried out on what is one of the most constant and conspicuous organs in our Australian earthworms. This is the spermiducal gland, which is characteristic without exception of the indigenous forms in Australia.

In addition to this, the study has included the histology of the various accessory structures and ducts associated therewith, for while the general macroscopic structure in these forms has been well described by Prof. Baldwin Spencer and Mr. J. J. Fletcher, the microscopic details have been comparatively unknown, except in the one form, *Megascolides australis*, also described by Prof. Spencer*. And here I would acknowledge my indebtedness to him for allowing me the use not only of his laboratory in the Melbourne University, but also of his large collection of Australian earthworms † and of literature thereon; also for much valued assistance on many occasions.

I have throughout made use of the generic divisions given by Beddard in his monograph of this group, this being the most easy means of reference.

The characteristic genera of earthworms in Australia are *Megascolides*, *Cryptodrilus*, *Diplorema*, *Fletcherodrilus*, *Diporochæta*, *Megascolex*, *Digaster* (including *Didymogaster* and *Perissogaster* (Fletcher)), and *Acanthodrilus*. The 32 species examined include a number from Queensland, New South Wales, Victoria, and Tasmania.

The male reproductive organs in these forms, as is well known, consist typically of three parts:—(1) two pairs of testes, generally

* Trans. Royal Society of Victoria, vol. i. pt. 1, 1888.

† The specimens of earthworms described by Mr. Fletcher were kindly sent by him to Prof. Spencer.

somewhat flat finger-like bodies attached to the anterior septum in segments 10 and 11. They are enclosed in a very delicate membrane connected with the peritoneal lining of the general body-cavity. The sperm mother-cells, which originate by multiplication of the cells of this peritoneal lining, pass out into (2) the seminal vesicles or sperm-sacs. These are generally found in pairs in segments 9 to 12, where they arise as out-growths of the septa, enclosing a small portion of the body-cavity. Here the sperm mother-cells develop so as to form by division the spermatozoa. These pass to the exterior by means of (3) two pairs of vasa deferentia. The latter open by means of two pairs of much-folded and ciliated funnel-shaped structures, from the segments in which the testes lie, and lead back through the following segments to open externally by a single pair of openings on segment 18, in the typical Australian Oligochæta. Associated with the external openings of these vasa deferentia are a pair of glands, the so-called "atria" or "prostates." The name "spermiducal glands," proposed for these glands by Beddard, is here retained as being the most appropriate. In addition, there are often present near the male pore other glands internally, or one or more "penial setæ."

These organs are in general constant throughout the group in many respects, but in detail they often vary widely in different species, both in structure and to a certain extent in position.

A. MACROSCOPIC CHARACTERS OF THE SPECIES.

I. MEGASCOLIDES.

1. *M. INTERMEDIUS* * (*Spencer*).

Only one pair of testes and of rosettes is present in this species. Sperm-sacs are found in segments 12 and 14.

The spermiducal glands (*sp.g.*, Pl. 14. fig. 3) are tubular in form and slightly coiled: they lie transversely to the body in segment 18, their ducts (*sp.d.*) opening on its external surface near the mid-ventral line. The duct of the spermiducal gland is almost straight and very muscular. The vas deferens on each side (*v.d.*) enters the gland-duct just where the latter leaves the gland.

Occupying the space internally, between and covering the two spermiducal ducts, and below the nerve-cord, is a white mass of

* Proc. Royal Society of Victoria, 1892, p. 132: *Cryptodrilus intermedius* (Spencer). Beddard, 'Oligochæta,' p. 492.

glandular cells, which may extend through one, two, or even four segments (*a.g.*, fig. 3), or, on the other hand, may rarely be absent altogether. The surface of this glandular mass has a mottled brown appearance, due to small patches of pigment. Its presence in these segments probably depends on the state of maturity of the individual.

2. *M. VICTORIÆ* * (*Spencer*).

Two pairs of testes and rosettes are present in segments 10 and 11; the sperm-sacs are situated on the posterior wall of segment 9 and on the anterior wall of segment 12. The spermiducal glands (*sp.g.*, fig. 4) are long, regularly-coiled tubes occupying segments 18 to 26, or even 29, one coil to each segment. The spermiducal duct is long and muscular, running transversely in a double loop towards the ventral surface in segment 18, where it opens. The two vasa deferentia of each side remain quite distinct for their whole length. They run alongside the gland-duct for some distance, and pass straight through the substance of the lower part of the gland, entering the gland-duct just before it leaves the gland. ■

3. *M. INSULARIS* † (*Spencer*).

Testes and rosettes in segments 10 and 11.

Sperm-sacs in segment 9 (posteriorly) and segment 12 (anteriorly).

Spermiducal glands very long coiled tubes in segments 18 to 27; duct long, muscular, and but slightly curved. The two vasa deferentia on each side join before reaching segment 18, and the single vessel so formed runs in the muscular wall of the gland-duct, and so enters the duct about one-third of its length from the gland.

4. *M. HOBARTENSIS* ‡ (*Spencer*).

Two pairs of testes and rosettes in segments 10 and 11.

Sperm-sacs in segments 9 (posteriorly) and 12 (anteriorly).

The spermiducal glands are long and coiled, extending through segments 18 to 24 or 25. The muscular duct from each resembles closely that of *M. insularis*, being long and slightly curved. The vasa deferentia also unite on each side before they

* Proc. Roy. Soc. Vict. 1892, p. 139: *Cryptodrilus victoriæ*, Spencer. Beddard, *loc. cit.* p. 488.

† *Ibid.* 1894, p. 41: *Cryptodrilus insularis*, Spencer.

‡ *Ibid.* 1894, p. 37: *Cryptodrilus hobartensis*, Spencer.

reach the level of the gland, the lower part of which they traverse, entering the spermiducal duct just as it leaves the gland.

5. *M. ATTENUATUS* * (*Spencer*).

Testes and rosettes, two pairs in segments 10 and 11.

Sperm-sacs in segments 9 (posteriorly) and 12 (anteriorly).

Spermiducal glands are two tubular, slightly-coiled glands lying transversely in segments 18 and 19, each with a short straight muscular duct. The two vasa deferentia of each side remain separate, running up within the muscular wall of the spermiducal duct, and entering the duct as it leaves the gland.

On each side, just behind the opening of the spermiducal duct, is a slightly muscular sac enclosing a long curved penial seta. As in *M. intermedius*, there is on the ventral surface internally, below the nerve-cord and between the two spermiducal glands, a great mass of unicellular glands, which may occupy one to three segments.

6. *M. AUSTRALIS* † (*McCoy*).

In this form, which has been so completely described by Prof. Spencer, there are two, or occasionally three, pairs of testes and two pairs of rosettes.

The sperm-sacs are found in segments 11, 12, 13, and 14, on the posterior wall in each case.

The spermiducal glands are very much coiled, tubular structures in segment 18; the duct of each is much coiled above and straight as it passes through the body-wall, receiving as it does so the two vasa deferentia.

7. *M. ROSEUS* ‡ (*Spencer*).

Testes two pairs in segments 10 and 11 with rosettes.

Sperm-sacs in segment 12 on the anterior wall.

Spermiducal glands tubular and closely coiled, either confined to segment 18 or extending into the segments before and behind, *i. e.* 17 and 19 (*cf.* fig. 5). The duct of the gland has strongly muscular walls, and is slightly curved. The vasa deferentia on each side do not unite, although they lie close side by side, deep down in the body-wall. They enter the spermiducal duct about halfway along its length.

* Proc. Roy. Soc. Vict. 1892, p. 155: *Megascolides attenuatus*, Spencer. Beddard, *loc. cit.* p. 491.

† McCoy, Prodromus Zoology of Victoria, Decade 1. Spencer, Trans. Roy. Soc. Vict. vol. i. pt. 1, 1888. Beddard, *loc. cit.* p. 495.

‡ Proc. Roy. Soc. Vict. 1892, p. 154. Beddard, *loc. cit.* p. 491.

8. *M. TUBERCULATUS* * (*Fletcher*).

Two pairs of testes and rosettes in segments 10 and 11.

Sperm-sacs on posterior wall of segment 9 and on the anterior wall of segment 12.

Spermiducal glands tubular and very much coiled, lying transversely in segment 18. The gland-duct is long, and curved proximally into an S-shape; it is embedded chiefly in the body-wall.

The two vasa deferentia enter each gland-duct at the same point at about half the length of the latter.

On each side, lying between the spermiducal duct and the mid-ventral line, are a pair of small, slightly muscular sacs, each enclosing a long, somewhat robust penial seta, which pierces the body-wall close to and on the inner side of the male opening.

II. *CRYPTODRILUS*.9. *C. ILLAWARRÆ* † (*Fletcher*).

One pair of testes and of rosettes are seen in segment 11: one pair of sperm-sacs also on the anterior wall of segment 12.

The spermiducal glands are apparently somewhat long and straight flattened structures, lying transversely in segment 18. The gland-duct is short and straight, almost completely enclosed in the ventral body-wall, through which it runs vertically downward to open on the surface. The vasa deferentia are two in number on each side; not one, as might be inferred from the presence of only one pair of testes and rosettes. These run at varying levels, the anterior one in the muscle of the body-wall, the posterior one at its edge, until they reach the level of the posterior half of segment 13, when the upper one descends and runs alongside the lower one in the muscle-layer back to segment 18. They then join just outside the wall of the spermiducal duct, and the single one thus formed runs down in the substance of the wall to open into the duct close to its external opening. At the inner end of each gland-duct is a pair of short narrow sacs, nacreous in appearance, from the muscle-fibres in their walls, and each containing a long curved penial seta (*s.*, fig. 24). These setæ are curiously hooked near their tips, and each opens independently of the others, through the body-wall,

* Proc. Linn. Soc. N.S.W. 1887, p. 611: *Notoscolex tuberculatus* (*Fletcher*).
Beddard, *loc. cit.* p. 494.

† *Ibid.* vol. iii. 1888, p. 1523. Beddard, *loc. cit.* p. 503.

on the inner side of, and sometimes slightly behind the male pores, and not through them as Mr. Fletcher has suggested.

10. *CRYPTODRILUS COORANIENSIS* * (*Spencer*).

Two pairs of testes and of rosettes in segments 10 and 11.

Sperm-sacs in segments 7, 8, 9, and 12. Those in segments 7 and 8 appear to be sometimes absent in specimens otherwise similar. In segments 10 and 11 the testes are not visible as distinct structures from the so-called sperm-sacs, but are seen in section to be simply much denser parts of the ventral portion of these sacs, immediately in front of each of the rosettes, which are also enclosed within the sac, and surrounded by developing sperm (*cf.* fig. 15). These sacs in segments 10 and 11 thus appear to correspond to what Beddard has termed "sperm-reservoirs." In segments 10 and 11 the sperm-reservoirs, and in segment 12 the sperm-sacs, form complete rings around the alimentary canal, those in segment 10 being much larger and less definite in shape than the others.

The spermiducal glands are bilobed or flat, both varieties occurring in a single individual. Each gland-duct is short and thick, and receives at half its length the two vasa deferentia which have distinct openings into it, on opposite sides of the duct.

III. DIPILOTREMA.

11. *D. FRAGILIS* † (*Spencer*).

Two pairs of testes and rosettes in segments 10 and 11.

One pair of sperm-sacs on the anterior wall of segment 12.

The spermiducal glands are long, coiled tubes extending through segments 15 to 25, and opening as usual in segment 18 (*cf.* fig. 6). The posterior end of the gland is turned back through four or five segments. The gland-duct is somewhat less muscular than usual, and runs straight down to the surface, where it opens. The two vasa deferentia on each side remain distinct until they reach the level of segment 17, when they join and open to the exterior in segment 18 in front of and quite distinct from the spermiducal duct. On the internal surface of the ventral body-wall in segments 16 to 22, between the spermiducal

* "Descriptions of Australian Earthworms," Part 1. Proc. Roy. Soc. Vict. vol. xiii. pt. 1.

† *Ibid.* vol. xiii. pt. 1.

ducts, is a glandular mass divided off into groups transversely by the septa, and supporting the nerve-cord. On the inner side of each spermiducal duct there are also a pair of slightly muscular sacs, each enclosing a curved penial seta. These open quite independently of each other and of the gland-duct, on the inner or ventral side of the latter.

IV. FLETCHERODRILUS.

12. *F. UNICUS* * (*Fletcher*).

Two pairs of testes and rosettes in segments 10 and 11.

Sperm-sacs in segments 9 and 10 (posteriorly) and 11, 12, and 13 (anteriorly). The gonads and rosettes appear distinct from the sperm-sacs in segments 10 and 11.

The spermiducal glands (*sp.g.*, fig. 2) are long tubular structures, lying transversely in segment 18, with the distal end somewhat coiled. Towards the mid-ventral line the tube becomes smaller and nacreous, marking the region of the duct, which then suddenly swells out, forming a well-marked muscular bulb, straight through the centre of which runs the duct. Into this duct, at the level of the nerve-cord, there opens on each side a single vas deferens, which arises anterior by the union of the two ducts which leave the two rosettes. The ventral end of the sac passes beneath the nerve-cord and the longitudinal muscle-band, and meets its fellow of the opposite side in the mid-ventral line. Here they unite and form a strongly muscular duct, which runs vertically downward and slightly forward to open on a papilla in the mid-ventral line of segment 18. It is possible that this common part may be partially protrusible.

V. DIPOROCHÆTA.

13. *D. COPELANDI* † (*Spencer*).

Two pairs of testes and rosettes in segments 10 and 11.

Sperm-sacs in segments 9 (posteriorly) and 11 and 12 (anteriorly).

Spermiducal glands are long, coiled tubular structures, and may extend through segments 17 to 23, though sometimes less.

* Proc. Linn. Soc. N. S. W. iii. (2) 1889, p. 1540: *Cryptodrilus unicus*, Fletcher. *Ibid.* iv. (2) 1890, p. 990: *Cryptodrilus purpureus* (Fletcher). Beddard, *loc. cit.* p. 481.

† Proc. Roy. Soc. Vict. 1892, p. 3: *Perichæta Copelandi* (Spencer). Beddard, *loc. cit.* p. 442.

The two vasa deferentia of each side remain quite distinct, though close together after segment 13. They enter the spermiducal duct, which is curved into a U-shape, near its external opening on segment 18. Close by, and on the inner side of each duct, and only visible under the microscope, are a pair of small and thin sacs, each containing two (or sometimes three) very fine, smooth, and slightly curved penial setæ, which open into the termination of the spermiducal duct by definite tubes lined with columnar cells.

14. *D. BAKERI* * (*Fletcher*).

Two pairs of testes and rosettes in segments 10 and 11.

Sperm-sacs in segments 9 (posteriorly) and 12 (anteriorly).

Spermiducal glands are tubular, somewhat coiled, and extend through four segments, 18 to 21 (fig. 1). The gland-duct is long and slightly curved, and very muscular. On the inner side of each duct is a pair of small sacs, each containing a penial seta surrounded by muscle-fibres. The division between the gland and the duct is more sharply marked than usual. The two vasa deferentia of each side join at the level of the prostate just before they enter the muscular wall of the duct, and so open into the duct itself at about half its length. Into the last portion of the spermiducal duct open by a pair of well-defined tubes the two penial setæ, which are stouter than in *D. Cope-landi*.

VI. MEGASCOLEX.

15. *M. FRENCHI* † (*Spencer*).

Two pairs of testes and rosettes in segments 10 and 11.

Sperm-sacs in segment 9 (posteriorly) and segment 12 (anteriorly).

The spermiducal glands are flattened and bilobed, and are situated in segments 18 and 19, one lobe in each (fig. 8). The whole surface of the gland is divided up into irregular or polyhedral areas, which, as will be seen later, correspond with certain points of internal structure. The septum separating segments 18 and 19 is continued between the two lobes of the gland, and is pierced by the branch of the duct on its way to the main gland-duct. The main gland-duct, which is in segment 18,

* Proc. Linn. Soc. N. S. W. ii. 1887, p. 616: *Perichæta Bakeri* (*Fletcher*). Beddard, *loc. cit.* p. 440.

† Proc. R. S. Vict. 1892, p. 9: *Perichæta Frenchi* (*Spencer*). Beddard, *loc. cit.* p. 379.

is formed by the union of two ducts, one from each lobe. The two vasa deferentia of each side unite in segment 13 to form one, which is larger in proportion than usual. This enters the spermiducal duct just at the union of its two main branches.

16. *M. FIELDERI* * (*Spencer*).

A pair of rosettes, in segment 11 are seen to be enclosed within a large membranous sac, in which, however, there was no indication of a testis.

Sperm-sacs in segment 12 are mushroom-shaped, and attached to the anterior wall by a definite stalk. In two specimens examined each sac was found to be filled with Gregarines.

The spermiducal glands are situated in segments 17 and 18; they are bilobed, one lobe in each segment (fig. 14). Occasionally a tendency to division into three lobes was seen in the larger and bifid character of the posterior lobe. The anterior is usually the smaller, and is often only united to the posterior one at the base by the branches of the gland-duct; while in other individuals again the gland is merely bifid, and confined to one segment. The surface of this gland, as in *M. Frenchi*, is divided up into numerous polygonal areas. The gland-duct is well marked, almost straight, and strongly muscular. As it passes down towards the ventral surface it curves slightly and enters a large hyaline muscular bulbus (fig. 14), within which the duct makes a double U-loop. The single vas deferens enters the muscular sac, and runs backwards and then alongside and behind the spermiducal duct, curving with it. The vas deferens joins the duct just after the latter has finally curved, to pass vertically downward to the external opening on segment 18. From its appearance, this last part of the spermiducal duct is probably protrusible. In one specimen, in which there was no prostate on one side, the vas deferens of that side simply ran straight to the surface in segment 18 without any increase of muscular fibres.

17. *M. TASMANICA* † (*Spencer*).

Two pairs of testes and rosettes in segments 10 and 11. The testes are large and finger-like.

Sperm-sacs in segments 9 (posteriorly) and 12 (anteriorly).

Spermiducal glands distinctly bilobed in segments 17 and 18; one lobe in each segment. In some individuals polygonal areas

* Proc. R. S. Vict. 1892, p. 19: *Perichæta Fielderi* (*Spencer*). Beddard, *loc. cit.* p. 379.

† *Ibid.* 1894, p. 47: *Perichæta tasmanica* (*Spencer*).

were visible on the surface. The spermiducal duct is large though not always very long, and is muscular. It receives one main branch from each lobe, the main duct lying in and opening on segment 18. The vasa deferentia, two on each side, are very large in proportion to the size of the animal. They run close side by side just embedded in the body-wall until, in segment 12, those on the right side unite, while those on the left do not unite till segment 14. They enter the spermiducal duct close to the union of the branches from the two lobes.

18. *M. HOGGII* * (*Spencer*).

Two pairs of testes and rosettes in segments 10 and 11.

Sperm-sacs in usual positions in segments 9 and 12.

Spermiducal gland in segment 18, bilobed and small; the surface appears smooth, without any markings. The duct is straight, or may be slightly curved, and is strongly muscular. The vasa deferentia, two on each side, enter the spermiducal duct close side by side, at about half its length.

19. *M. DENDYI* † (*Spencer*).

Two pairs of testes and rosettes in segments 10 and 11.

Sperm-sacs in segments 9 (posteriorly) and 12 (anteriorly).

Spermiducal glands in segments 18 and 19, may be flattened with but the smallest indication of a second lobe, or they may be clearly divided into two lobes (fig. 9). The surface of the gland is sometimes very much grooved, though not in any regular fashion, and having no relation to internal structure. The duct is single, *i. e.* it does not branch outside the gland-substance; it is long and curved into almost an S-shape in some cases, and at others forming three or four loops. The two vasa deferentia of each side remain quite distinct and enter the spermiducal duct side by side, just where it leaves the gland.

20. *M. DORSALIS* ‡ (*Fletcher*).

Two pairs of testes and rosettes in segments 10 and 11, both testes and rosettes being very large.

* Proc. R. S. Vict. 1892, p. 6: *Perichæta Hoggii* (Spencer). Beddard, *loc. cit.* p. 379.

† *Ibid.* p. 12: *Perichæta Dendyi* (Spencer). Beddard, *loc. cit.* p. 380.

‡ Proc. Linn. Soc. N. S. W. vol. ii. 1887, p. 618: *Perichæta dorsalis* (Fletcher). Beddard, *loc. cit.* p. 376.

Sperm-sacs are conspicuous globular bodies in segments 9 (posteriorly) and 11 and 12 (anteriorly).

The spermiducal glands vary in position, and to a certain extent in shape. In one individual each was distinctly tubular, occupying segments 18 and 19, the wider portion in segment 19 being coiled. In this also the duct was very short, and completely embedded in the body-wall. In a second individual, the gland was much wider in proportion to its length, and appeared at first as a single flat elongated body in segments 18, 19, and 20, the duct forming a double-U curve. In the third specimen (fig. 10) the gland appears as a wide flat tube in segments 18, 19, 20 and 21; slightly curved in the first and last segments. The duct in this case was very short. The surfaces of the glands in the first and second individuals were quite smooth, apart from grooves incidental to curving. But in the third individual, the gland clearly showed an irregular division of the surface into areas exactly similar to those on the gland of *M. Frenchi*. The two vasa deferentia of each side enter the gland-duct on opposite sides at half its length from the exterior. The external opening is situated on a very strongly-marked papilla. In this papilla are situated two distinct sets of glands connected with the external openings.

21. *M. RUBRA* * (*Spencer*).

Testes and rosettes, two pairs in segments 10 and 11.

Sperm-sacs in segments 9 (posteriorly) and 12 and 14 (anteriorly).

Spermiducal glands bilobed, lying entirely in segment 18, the posterior wall of which is pushed back. The spermiducal duct is long and coils slightly as it leaves the gland. The two vasa deferentia of each side unite about segment 13 to form one on each side, which runs up the wall of the spermiducal duct and enters it just inside the gland.

22. *M. MINOR* † (*Spencer*).

Segments 10 and 11 are occupied by what appear to be large sperm-sacs filled with masses of developing sperm. At the base of those near the nerve-cord on each side is a small spherical,

* Proc. R. S. Vict. 1892, p. 8: *Perichæta rubra* (Spencer). Beddard, *loc. cit.* p. 379.

† "Descriptions of Australian Earthworms," Pt. 1. Proc. R. S. Vict. vol. xiii. pt. 1.

denser and more compact portion, which probably represents the true testis. The rosettes, though covered with sperm, were not seen to be included in the membrane enclosing the testes—though in other respects these agree with the sperm-reservoirs of Beddard.

The true sperm-sacs are very compact saccular structures in segments 9 (posteriorly) and 12 (anteriorly), and sometimes in 13 (anteriorly), those in segment 12 being the least saccular of the three.

The spermiducal glands are bilobed, or sometimes merely flat, and bifid structures in segment 18, the anterior wall of which becomes somewhat pushed out of position. The duct is small and S-shaped, and less muscular than usual. The vasa deferentia unite in segment 12 to form one on each side, which enters the spermiducal duct as it leaves the gland.

23. *M. INTERMEDIUS* * (*Spencer*).

As in *M. minor*, though even to a more marked extent, the sperm-reservoirs are developed one on each side in segments 10 and 11, enclosing masses of developing sperm. The testes and rosettes, the latter of which are distinctly "Maltese-cross" in shape, are enclosed in the same membrane. In both segments each reservoir (*cf.* fig. 15) is divided off into two parts, the larger ventral part enclosing testis and rosette. The septum between segments 8 and 9 is lost, being merely represented by a few fibrous cords. Occasionally also that between segments 9 and 10 is absent, in which case the sperm-reservoir of segment 10 is lost, the rosette alone being present. The sperm-sac usually found on the posterior wall of segment 9 is absent; a pair is present in segment 12 (anteriorly).

The spermiducal gland appears to be generally bilobed, with a strongly-marked U-shaped duct, the whole lying in segment 18. In one individual the gland on one side was flattened and irregular in shape, showing only a slight division into two parts. The duct was coiled, and the two vasa deferentia of that side opened into the duct a little way from the gland. On the other side the gland was absent, and the two vasa deferentia united in segment 18 and formed, with the addition of a thick wall of muscle-fibres, a duct corresponding in size and position with that on the other side.

* "Descriptions of Australian Earthworms," Pt. 1. Proc. R. S. Vict. vol. xiii. pt. 1.

24. *M. ILLIDGEI* * (*Spencer*).

Two pairs of testes and rosettes as usual in segments 10 and 11.

Sperm-sacs in segments 9 (posteriorly) and 12 (anteriorly). Spermiducal glands are bilobed and flattened, and wrap round the alimentary canal; their ducts are short but S-shaped.

The two vasa deferentia of each side unite only as they reach the level of the spermiducal duct. The single vessel thus formed enters the wall of the duct, and runs up in it, uniting with the gland-duct just as it emerges from the gland.

VII. DIGASTER.

25. *D. ARMIFERA* † (*Fletcher*).

Two pairs of testes and rosettes in segments 10 and 11.

Sperm-sacs in segments 9 (posteriorly) and 12 (anteriorly). In one individual the whole of the segments 10 and 11 was filled with masses of developing sperm in which the rosettes were embedded. No definite membrane enclosed the mass, nor could any special representative of a testis be found, even in section; but it may probably be regarded as a sperm-reservoir. The size of the true sperm-sac in segment 12 is quite abnormal, and has almost completely closed up segment 13 by the pushing back of its anterior wall. The blood-vessels in this segment were also unusually large. In one specimen sperm-sacs were also present in segments 14 and 15 (anteriorly).

The spermiducal glands are present in segments 17, 18, and 19, or sometimes only in segment 18, which is then much extended. The glands are lobate, usually with three lobes more or less divided off. The whole surface is distinctly marked off into similar irregular areas to those seen in *Megascolex Frenchi*. The gland-duct is comparatively large and long, and is slightly curved (fig. 13). The two vasa deferentia of each side run very close together in the body-wall, and enter the spermiducal duct just after it leaves the gland.

Lying posterior to the gland-duct are two narrow sacs with slightly muscular walls. Each of these contains two well-marked penial setæ in a well-marked sheath. Each is curved and long, and is ornamented near the tip with numerous little short spines, as described by Mr. Fletcher, ending in a chelate point. The

* "Descriptions of Australian Earthworms." Proc. R. S. Vic. vol. xiii. pt. 1.

† Proc. Linn. Soc. N. S. W. i. (2) 1887, p. 947. Beddard, *loc. cit.* p. 486.

setæ reach the surface through a small duct opening into the spermiducal duct just before that duct reaches the external opening.

26. *D. GAYNDAHENSIS* * (*Spencer*).

Two pairs of testes and rosettes in segments 10 and 11.

Sperm-sacs large in segments 9 (posteriorly) and 11 and 12 (anteriorly). Spermiducal glands in segment 18 are small and flat. The duct is small and short, running straight down to the external opening on 18. The two vasa deferentia on one side join to form one duct near the gland. Those on the other side apparently remain distinct. In each case they traverse the substance of the spermiducal gland and run down inside the wall of the duct, with which they unite halfway to the exterior.

27. *D. MINOR* † (*Spencer*).

Two pairs of testes and rosettes in segments 10 and 11.

Sperm-sacs in segments 9 (posteriorly) and 12 (anteriorly)—in one specimen in segments 9 and 11. In segments 10 and 11 in the first specimen, the testes and rosettes were enclosed in true sperm-reservoirs.

The spermiducal gland is completely bilobed and not flattened: the duct is formed by the union of a branch from each half. The vasa deferentia, two on each side, having remained separate through their whole length, pass straight through the substance of the lower part of the anterior lobe of the spermiducal gland before entering the duct of that branch just before it unites with its fellow from the posterior lobe.

28. *D. BRUNNEUS* ‡ (*Spencer*).

One pair of testes in segment 10, and two pairs of rosettes in segments 10 and 11. The anterior rosettes are very small indeed.

Sperm-sacs in segment 12 (anteriorly).

Spermiducal glands larger than in *D. gayndahensis*, flattened and slightly bilobed. The duct is small and less muscular than usual, and runs straight into the body-wall. The two vasa

* "Descriptions of Australian Earthworms," Proc. R. S. Vict. vol. xiii. pt. 1.

† *Ibid.* pt. 1, Proc. R. S. Vict. vol. xiii. pt. 1.

‡ *Ibid.* pt. 1, Proc. R. S. Vict. vol. xiii. pt. 1.

deferentia of each side remain quite distinct, and enter the spermiducal duct as it leaves the gland.

29. *D. SYLVATICA* * (*Fletcher*).

Two pairs of testes and rosettes in segments 10 and 11.

Sperm-sacs are racemose structures in segments 9 (posteriorly) and 12 (anteriorly). This differs considerably from the original description, where the structures in segments 9 and 12 are called testes and described as "smooth and white bodies drawn out above into digitate processes tapering into fine points," while no sperm-sacs were mentioned whatever.

The organs in segments 9 and 12, here called sperm-sacs, and which have both the position and appearance of those structures in other forms, are conspicuous, white, and greatly mammillated. Also there are distinct digitate though small testes in their normal positions on the anterior wall of segments 10 and 11.

Spermiducal glands are bilobed and large. The duct is short and muscular, and embedded in the body-wall. The two vasa deferentia of each side enter the spermiducal duct as it leaves the gland.

30. *D. EXCAVATA* † (*Fletcher*).

In one specimen, testes and rosettes were present in segments 10 and 11.

The sperm-sacs were grape-like, in segments 9 (posteriorly) and 12 (anteriorly).

In this the spermiducal gland consisted of a long tubular structure, the anterior part lying in segment 18, considerably larger and flatter than the posterior part which extended back in segments 18 and 19. The duct leaves the gland at the beginning of the tube and is short, running down obliquely to open on the surface. The duct is less muscular than usual, and into it at the base of the gland opens the single vas deferens formed by the union on each side of the two vasa deferentia. On the inner side of the duct and opening into its lower portion are two slightly muscular seta-sacs, each containing one long seta.

In a second specimen there was no appearance of testes as distinct from the sperm-reservoirs, which occupied segments 10

* Proc. Linn. Soc. N.S.W. vol. i. (2) p. 558: *Didymogaster sylvatica* (*Fletcher*). *Beddard, loc. cit.* p. 487.

† *Ibid.* vol. ii. (2) p. 383: *Perissogaster excavata* (*Fletcher*). *Beddard, loc. cit.* p. 486.

and 11 and enclosed the rosettes. The spermiducal gland was of a constant width throughout.

A third individual resembled the second in every respect, except that on one side the spermiducal gland was turned forward, lying in segment 18 entirely. As will be seen later, this differs somewhat from the original description. Around the spermiducal duct the body-wall is much thickened owing to the presence in it of groups of long unicellular glands, whose ducts open in groups on the surface around the male opening.

31. *D. QUEENSLANDICA* * (*Fletcher*).

Two pairs of testes and rosettes in segments 10 and 11. Sperm-sacs very small in segments 11 and 12 (anteriorly). The spermiducal gland is flat in some specimens and well-developed (Pl. 14. fig. 11), while in others it appears to be either very small and tubular (fig. 12), or absent altogether, as in six specimens of those examined. In one of these specimens neither sperm-sacs nor testes could be seen, probably pointing to its immature condition. The two vasa deferentia, which along their length are separated by a short distance, enter the gland-duct quite separately at about half its length.

VIII. ACANTHODRILUS.

32. *A. SYDNEYENSIS* (*Fletcher*).

One pair of rosettes in segment 11. Masses of sperm in segments 11 and 12, the first probably representing a sperm-reservoir, and the second sperm-sacs. Nothing comparable to a testis could be seen. The single vas deferens of each side runs back along the edge of the body-wall, and opens independently of the spermiducal glands on segment 18.

The spermiducal glands (*sp.g.*, Pl. 14. fig. 7) are two pairs of long, coiled tubular structures, one pair opening to the surface in segment 17, and the other in segment 19. Both extend back as far as segment 26. The muscular duct of each gland extends from its external opening back through about $1\frac{1}{2}$ segments, and then passes into the second region which extends through another $3\frac{1}{2}$ segments, while the most distal glandular region is found in the last three of these segments. The glands lie near the nerve-cord on each side, passing through the ventral opening in the septa with the nerve-cord and ventral blood-vessel.

* Proc. Linn. Soc. N. S. W. vol. iii. (2) p. 1529: *Perissogaster queenslandica* (Fletcher). Beddard, *loc. cit.* p. 485.

B. GENERAL MACROSCOPIC FEATURES.

I. *Testes and Sperm-sacs.*

The position of the testes in segments 10 and 11 appears nearly constant throughout the Australian genera. Occasionally we find that there is but one pair of testes, in which case it is situated in segment 11, e. g. *Cryptodrilus illawarræ* and *Megascolides intermedius*, or rarely in segment 10 as in *Digaster brunneus*. Rarely less than two pairs of rosettes are present, e. g. *Megascolex Fielderi*, *Cryptodrilus illawarræ*, and *Megascolides intermedius*; though the anterior pair may be very small (e. g. in *Digaster brunneus*). Very often, as in *Megascolex intermedius*, *M. minor*, *Digaster minor*, and *Cryptodrilus cooraniensis*, the testes or rosettes, or both, are enclosed within sperm-reservoirs. There is, when present, one of these structures on each side in contrast to the median position of the typical "sperm-reservoirs" to which the name was originally given by Beddard. Each reservoir may or may not be divided by a connective-tissue septum into two or more chambers (cf. *s.r.* Pl. 14. fig. 15), the ventral of which is larger and contains the rosette (*r.*), and also the denser, more compact, and more darkly-staining portion, which represents the testis in such cases except in *Digaster armifera*, where it is absent. The rosette is, rarely, not enclosed in this sac, when it is present, as in *Megascolex minor*; but since it nevertheless contains the "testis," it may be regarded as answering to Beddard's definition of a "sperm-reservoir" as a sac enclosing the gonads and the rosettes. The true sperm-sacs are usually found on the posterior wall of segment 9, and on the anterior wall of segment 12. In addition to this, there is sometimes a pair of true sperm-sacs in segment 11, e. g., in *Digaster gayndahensis*, *Diporochæta Cope-landi*, and *Megascolex dorsalis*. Sometimes that in segment 12 only may be present, as in *Digaster brunneus*, *Megascolex Fielderi*, *Cryptodrilus illawarræ*, *Diplostrema fragilis*, and *Megascolides roseus*. In other forms, that in segment 9 may be absent, and present in segments 11 and 12, e. g. *Digaster queenslandica*. In *Megascolex rubra* they are found in segments 9, 10, and 14; in *Megascolides australis* in 11, 12, 13, and 14; in *Megascolides intermedius* in 12 and 14; in *Digaster armifera* in 9, 12, 14, and 15; and in *Fletcherodrilus unicus* in segments 9, 10, 11, 12, and 13. Those occurring in segments 9 and 10

are attached to the posterior wall of the segment, and those in segments behind 10 to the anterior wall of the segment. These sperm-sacs vary in form as well as in position. Sometimes they form definitely shaped masses enclosed in a firm membrane. In this case, they are simply lobed or mammillated, or form a ring around the alimentary canal. At other times they are much looser, racemose structures, when the investing membrane is easily broken. Again, the whole cavity of the segment may be completely filled by a mass of seminal cells, obliterating the cavity of the succeeding segments by backward pushing of the septum. In several instances Beddard has cast doubt on the character of the sacs in segments 13 and 14 when so existing, preferring to regard them as egg-sacs rather than sperm-sacs as described. In no species which I have examined has there been any sign of ova in such a position, these sacs invariably containing developing sperm.

II. Spermiducal Glands.

These are usually found in segment 18 and sometimes in contiguous segments, only very rarely extending in front of segment 18. The two main types of external form are tubular and lobate (including flat and undivided forms).

(1) *Tubular Glands*.—These lie either transversely to the body, when they are generally confined to segment 18; but in some species they may, when mature, extend as far back as segment 26. They are usually slightly coiled, but in some cases, e. g., *Megascolides roseus* and *M. australis*, they are twisted into an almost inextricable mass, lying in segment 18. They are characteristic of the following genera:—*Megascolides*, *Cryptodrilus* (partly), *Fletcherodrilus*, *Diporochæta*, and *Acanthodrilus*. With regard to *Digaster*, it will be noted that the two species *D. excavata* and *D. queenslandica* are somewhat different from the remainder of the genus, more especially the former species. They have been described as bilobed, with a flattened lobe anteriorly and a long tubular portion posteriorly. In the specimens of *D. excavata* examined by me only tubular “prostates” have been seen, though in one individual a band of connective-tissue in the position described for the gland-duct might possibly be mistaken for a duct. It, however, does not contain any duct whatever, the true gland-duct leaving the

front end of the tubular gland. In *D. queenslandica*, as before stated, the majority of specimens have no spermiducal gland; in others it is a small, shortened, flattened tube (fig. 12), while yet another has a large well-developed flattened single lobe (fig. 11). In *Cryptodrilus illawarræ* the gland forms, as will be seen later, a transitional stage between such a tubular gland as that of *Diplo-trema fragilis* and the second group of forms. In *Acanthodrilus sydneyensis*, as is typical of the genus, there are two pairs of tubular prostates lying longitudinally. The first pair open on segment 17, and the second pair on segment 19, and both run backwards, coiling somewhat as they go, as far as segment 26.

(2) *The Lobate Glands*, including single-lobed, bilobed, and trilobed forms, are characteristic of the remaining genera, viz., *Megascolex Digaster* (excluding *D. queenslandica* and *D. excavata*), and *Cryptodrilus*.

Among these, the external form of the gland in *Megascolex dorsalis* would suggest the possibility of its being an intermediate condition between the tubular and lobate forms, as also that of *Cryptodrilus illawarræ* (vide infra). These glands usually occupy but one segment, that in which they open, 18; but often the posterior lobe is found in segment 19 separated from the anterior lobe by the septum between these two segments.

III. Ducts (Vasa Deferentia and Spermiducal Ducts).

There is a certain amount of variation in the arrangement of each of these ducts, and in their relations one to the other.

(1) *The Spermiducal Duct*.—The main part of the duct, which is usually well supplied with circular muscles, both in the lobate and tubular forms, may be—(1) short and straight or but slightly curved: e. g., *Megascolex tasmanica*, *M. Hoggii*, *Diporochæta Copelandi*, *Cryptodrilus cooraniensis*, *Megascolides intermedius*, *M. attenuatus*, *Digaster minor*; occasionally being confined entirely within the body-wall, e. g., *Digaster brunneus*, *D. gayndahensis* from Queensland, and *Cryptodrilus illawarræ*.

(2) It may be long and more or less curved, sometimes but slightly, as in *Megascolides roseus*, *M. victoriae*, *M. insularis*, *M. hobartensis*, *Megascolex rubra*, and *Diporochæta Bakeri*; at other times it is much longer, forming a U-shaped loop, e. g. *Megascolex intermedius*, or, again, forming a double loop as in *Megascolex dorsalis* and *M. Dendyi*, &c. (3) In the lobate forms

the main duct may either (a) leave the substance of the gland before the branches from the separate lobes have united, as in *Megascolex Frenchi*; or (b) it may leave the gland as a single duct, as in the great majority of cases, e. g., *Megascolex Dendyi*, *M. tasmanica*, or *Digaster armifera*.

Another variation connected with the spermiducal duct is in the presence of a muscular swelling or bulbus on each side in *Megascolex Fielderi* and *Fletcherodrilus unicus*. In the latter it partakes more of the nature of a swelling caused by an enormous and somewhat sudden thickening of the muscular layer of the duct-wall, straight through which the duct runs on its way to join its fellow of the opposite side, and open to the surface. In *Megascolex Fielderi*, however, it is different. The bulbus is almost spherical (*m.b.*, Pl. 14. fig. 14), and similar in size to that in *F. unicus*. The duct is sharply bent just before it enters the side of the bulbus, which it does obliquely. Within the bulbus the duct makes a complete coil, the vas deferens accompanying it until it opens into the duct a short distance from the external opening.

(2) *Vasa deferentia*.—In accordance with the usual presence of two pairs of rosettes, there are generally two pairs of vasa deferentia. Even when the second pair of rosettes is absent, the two vasa deferentia are usually present on each side. Rarely there may be only one pair of vasa deferentia, e. g., *Megascolides intermedius* and *Megascolex Fielderi*. They may join when there are two on each side as soon as possible after the 11th segment, *i. e.* in the 12th, e. g., *Megascolex tasmanica*, *M. minor*; or they may unite in the 13th or 14th segments, not always at the same level on the two sides, e. g., *Fletcherodrilus unicus*, *Megascolex Frenchi*, *M. rubra*. They may join just before they reach the spermiducal duct, as in *Megascolides insularis*, *M. hobartensis*, *Cryptodrilus illawarræ*, *Diplostrema fragilis*, *Diporochæta Bakeri*, *Megascolex Illidgei*, *Digaster gayndahensis*, *D. excavata*; or they may join as they enter the duct, e. g., *Megascolides attenuatus*, *M. australis*, *M. tuberculatus*, *Diporochæta Copelandi*, *Megascolex Hoggii*, *M. Dendyi*, *M. intermedius*, *Digaster armifera*, *D. sylvatica*, *D. minor*, *D. brunneus*; or they may open into the duct quite independently of each other, *e. g.*, on opposite sides of the duct—such are *Megascolides victoriæ*, *M. roseus*, *Cryptodrilus cooraniensis*, *Megascolex dorsalis*, *Digaster queenslandica*.

Variations in the relations of the spermiducal duct to the vasa

deferentia fall into four groups. (1) Those forms in which they unite just where the gland-duct leaves the gland, e. g., *Megascolex tasmanica*, *M. Dendyi*, *M. rubra*, *M. minor*, *M. intermedius*, *M. Illidgei*, *Megascolides intermedius*, *M. attenuatus*, *Digaster armifera*, *D. excavata*, *D. minor*, *D. brunneus*, and *D. sylvatica*. Sometimes the vasa deferentia traverse the substance of the lower part of the spermiducal gland before they join the gland-tube, e. g., in *Digaster minor*, *Megascolides victoriae*, *M. hobartensis*, and *Megascolex rubra*. (2) Those in which the vasa deferentia enter the gland-duct at some point along the length of the latter: e. g., *Megascolex Frenchi*, *M. Fielderi* ($\frac{2}{3}$), *M. dorsalis* ($\frac{1}{2}$), *M. tasmanica*, *M. Hoggii*, *M. Dendyi* ($\frac{1}{2}$), *Diporochæta Copelandi* ($\frac{2}{3}$), *D. Bakeri* ($\frac{2}{3}$), *Fletcherodrilus unicus* ($\frac{2}{3}$), *Megascolides insularis* ($\frac{1}{3}$), *M. australis*, *M. roseus* ($\frac{1}{2}$), *M. tuberculatus*, and *Digaster queenslandica*, *D. gayndahensis*, and *Cryptodrilus cooraniensis*. (3) Those forms in which they join just before the external opening, or they may even open together on the surface, e. g., *Cryptodrilus illawarræ*, and sometimes *Diporochæta Copelandi*. (4) Those in which the vasa deferentia open quite independently of the spermiducal openings, e. g. *Diplotrema fragilis*—in front, but on the same segment; and in *Acanthodrilus sydneyensis*, on different segments.

It will be seen from the examples given in the second group, that there are several exceptions among these Australian forms to the statement made by Beddard that the vasa deferentia enter the gland-duct at its commencement in the Perichætida.

Associated with these ducts are to be seen, in certain genera and species, penial setæ. These are usually situated two on the inner side of each spermiducal duct. They are enclosed in a sheath within slightly muscular sacs—usually each sac only contains one seta, e. g., in *Megascolides attenuatus* (one on each side of the body), *M. tuberculatus*, *Cryptodrilus illawarræ*, *Diporochæta Bakeri*; but sometimes there may be two or even more in each sac, e. g., in *Diporochæta Copelandi* and *Digaster armifera*. These setæ may open by definite ducts into the cavity of the spermiducal duct and so reach the surface, e. g. in *Diporochæta Bakeri*, *D. Copelandi*, and *Digaster armifera*. At other times they simply protrude straight through the body-wall, independently of the duct, e. g., *Diplotrema fragilis*, *Megascolides tuberculatus*, *Cryptodrilus illawarræ*. They are larger than usual in *Megascolides tuberculatus*, *Diporochæta Bakeri*, and *Digaster*

armifera, and thinner than usual in *Diporochæta Copelandi*. In all, except *Cryptodrilus illawarræ* and *Digaster armifera*, they are smooth and slightly curved. In *C. illawarræ* (Pl. 15. fig. 24) they are curiously bent back or recurved near the tip; while in *Digaster armifera* (as already described by Mr. Fletcher) the tip is beset with five spines, and ends in a double chelate joint

C. HISTOLOGY.

I. Spermiducal Glands.

Typically each gland is a hollow structure, the body-wall being composed of long glandular cells, with a columnar cell-lining and covered by peritoneal membrane. Though there are considerable differences in the microscopic structure of the spermiducal gland in various forms, yet there is a certain amount of constancy in the relations of the external and internal structure of the gland. Thus the variations in its histology fall chiefly into two main groups, corresponding (1) to the tubular forms, and (2) to the lobate forms.

1. *The Tubular Forms* (Pl. 14. fig. 16).—Here there is a central duct running the whole length of the gland, and directly continuous to the exterior. This duct is lined throughout by epithelium generally of ordinary columnar cells (*e.e.*), with a nucleus at the inner end of each (fig. 17), or sometimes of cubical cells (fig. 16). The inner ends of the cells are usually more or less horny, while the nuclei are usually clearly visible even when the boundaries of the cells are not so (fig. 17). In *Megascolides australis*, however, as previously described by Professor Spencer, these lining-cells are more granular in appearance, staining deeply and rarely showing any nuclei. Outside this lining is often a small amount of connective-tissue with small blood-vessels. The outermost layer of the wall of the duct making up the bulk of the gland is composed chiefly of coarsely granular gland-cells (*g.c.*, Pl. 14. fig. 16 & Pl. 15. fig. 17). Each of these has a pear-shaped outer end, containing a nucleus often pushed to one side: it has a long narrow duct-like inner end which opens into the lumen of the gland, between the cells of the columnar lining—sometimes singly, *e.g.*, in *Megascolides roseus*, *M. australis*, *M. attenuatus*, *M. insularis*, *M. hobartensis*, and *Diplorema fragilis*; and sometimes in groups, especially where the lining is at all horny, *e.g.* in *Megascolides intermedius* (fig. 17),

M. victoriæ, *M. tuberculatus*, *Digaster excavata*, *Fletcherodrilus unicus*, *Diporochæta Copelandi*, and *D. Bakeri* (occasionally in the latter they appear singly).

In some forms there are a limited number of cells which are generally scattered and are similar to the gland-cells around them, except that they are more granular and stain very much more readily with methylene-blue than the others, and are therefore very conspicuous, *e. g.* in *Megascolides victoriæ* and *Fletcherodrilus unicus*, in both of which cases they are very numerous; also in *Digaster armifera* and *Diporochæta Bakeri*. At other times similarly staining cells form a more or less distinct layer at about half the thickness of the wall of the gland. These cells have a more rounded club-shaped end than the ordinary gland-cells, and are very well-marked in *Megascolides insularis* (Pl. 14. fig. 16) and *M. hobartensis*. The blood-vessels in these forms are sometimes found in the connective-tissue immediately around the columnar-cell lining; but often the main blood-vessel runs down the side of the gland, branching there and sending in fine capillaries amongst the glandular cells (*b.v.*, Pl. 15. fig. 17). The forms *Cryptodrilus illawarræ*, *Megascolex dorsalis*, and *Digaster excavata* will be described with the lobate forms.

In *Acanthodrilus sydneyensis* (Pl. 15. fig. 18) the structure of the three parts of each tube is as follows:—The proximal part is the gland-duct (fig. 18 *a*), which as usual is lined by columnar cells, the cell-outlines being rarely seen while the nucleus is large and distinct. The muscle-layer forming the thickness of the wall (*c.m.*) is composed, as in other forms, chiefly of circular fibres.

The next part forms an intermediate region between the duct and the glandular part proper. The lining of non-glandular epithelial cells is continued back from the duct (fig. 18 *b*). The glandular cells (*g.c.*) are quite distinct in appearance from those previously described. They are almost columnar in shape, with an inner slightly rounded end and a nucleus near their outer end, surrounded by the granular cell-contents. This is succeeded by the third and most distal part (fig. 18 *c*)—the most glandular. This is most striking in appearance, owing to the rapidity with which the cell-contents stain in methylene-blue, as may be seen on reference to the figure, where it is indicated by the depth of the shading. The facts show that the deeply-staining material (mucous or other secretion) is situated variously at the inner or outer end of the cell; and it may be

inferred that in the latter case it has not yet made its way to the cavity of the gland; while in the former it is just about to be passed out into that cavity, as the outer part of the cell in these cases is very finely granular, and does not take the methylene-blue at all readily. The cells are much larger than those seen in other forms, and, by the irregularity in shape of their inner ends, they make the cavity of the gland in this region very uneven, though of greater calibre than the intermediate portion. The blood-vessel runs up alongside the wall of the gland and branches on the surface. It will be found that this differs considerably from the description given by Beddard of the spermiducal gland of *Acanthodrilus* among other genera. *Acanthodrilus* is described by him as being similar to other genera of Megascolicidæ, such as those having tubular spermiducal glands, *i. e.* the Cryptodrilidæ and Perichætidæ, and all but one of the Acanthodrilidæ. That this is not so in this species is evident. In the first place, the cells of the columnar lining, even in the intermediate portion, are not granular, the nucleus only being generally visible, and indeed this is by no means a constant character in many of the genera, as before described. There is further no columnar-cell lining at all in the glandular part proper of this *Acanthodrilid*. Again, the glandular cells here are quite distinct in shape and appearance from the pear-shaped cells with long duct-like inner ends, found so constantly in such genera as *Megascolides*, *Diporochæta*, and the ordinary *Acanthodrilids*. They are here moreover only one layer thick. Even in the intermediate portion the gland-cells are more like those in the glandular part proper, than like those found in the genera above named.

2. *The Lobate Forms*.—These show in microscopic section a distinct and characteristic lobular arrangement, typically without any central tube. The lobules are more or less well-defined accordingly as the whole gland is less or more compact, since in the more closely-packed glands the cells of contiguous lobules have a tendency to overlap, thus masking to a certain extent the radiate appearance so conspicuous in the looser forms. The lobules, especially in the latter case, are separated by a small amount of connective-tissue (Pl. 15. fig. 19). In this there run the blood-vessels of the gland (*b.v.*), which are often very numerous and definite, *e.g.* in *Digaster brunneus*, and at other times have more the nature of lacunæ; the very fine terminal branches of the

gland-duct are also to be found in this connective-tissue. The latter are lined by a well-marked cubical epithelium surrounded by a few muscle-fibres. Each lobule has typically a radiate appearance, with sometimes a small lacuna or space (*l.l.*) in its centre, *e. g.* in *Megascolex Dendyi*, *M. tasmanica*, and *M. dorsalis*, which is however generally obliterated by the approximation of the inner ends of the cells. In very rare cases, a communication can be traced between it and one of the terminal branches of the gland-duct (as in fig. 20). In no instance was an epithelium of any kind to be seen around the central lacuna. The cells forming the substance of the lobules are of three kinds:—(i) The chief are those having the appearance of ordinary long narrow gland-cells with swollen outer ends, which contain large darkly-staining granules with generally a nucleus. (ii) The second group of cells are a number which appear to be quite empty and rarely showing a nucleus: they are probably simply cells which have discharged their contents into the gland-duct. (iii) Here again in some forms, *e. g.* *Megascolex Frenchi* and *Digaster queenslandica*, we find the cells seen in the tubular forms which stain readily with methylene-blue, and which serve here to accentuate the radiate appearance of the lobules, especially in *D. queenslandica*. The inner ends of the first and second sets, and of the third when present, come together in the centre of the lobule and evidently pour their contents into the gland-duct by means of the lacuna and duct before mentioned.

As before stated, the three species *Cryptodrilus illawarræ*, *Megascolex dorsalis*, and *Digaster excavata*, are intermediate forms between the tubular and lobate glands. In the two former there is a well-marked central duct running the whole length of the gland (fig. 24), and lined by columnar cells with a cuticular edge as usual in tubular forms. The main mass of the gland, however, is made up of lobules sometimes indistinctly separated from one another. In the centre of each lobule is a lacuna, which is connected with the central duct by a complex series of branches. Blood-sinuses run between the lobules. In *Digaster excavata* the branching is very much less complicated. There is but one series of branches from the central tube to form lobules, which are sometimes but seven or eight in number in the circumference of the gland. The central duct with its columnar lining is very conspicuous. It will be noted that this intermediate character agrees entirely in the first two cases with

what might have been expected from the external form, for it is often difficult to know to which group to refer the glands in these species by merely examining the outside of the gland.

II. Accessory Glands.

(1) Glands found within the cœlom, as in *Megascolides intermedius*, *M. attenuatus*, and *Diploptrema fragilis*. These include two distinct types. In *Megascolides intermedius* and *M. attenuatus* the glandular masses occupy the internal surface of the ventral body-wall between the spermiducal ducts. In the former, *M. intermedius* (Pl. 14. fig. 3), these structures (*a.g.*) vary in the number of segments they occupy, *e.g.* from two to four segments, or they may even be absent altogether. In *M. attenuatus* they were found to occupy three segments—17, 18, 19. They consist (Pl. 15. fig. 21) of a mass of long unicellular glands covered by the thin peritoneal membrane; the gland-cells have pear-shaped outer ends, with granular contents and distinct nuclei. The long narrow duct-like inner ends of these cells (*g."c."*) run down through the longitudinal and circular layers, and open on the ventral surface between the columnar cells of the epidermis. In *M. attenuatus* the gland-cells at the sides of the mass are much (sometimes two or three times) longer than those in the centre, otherwise they resemble those in *M. intermedius*. In each case the nerve-cord runs above, and is supported by the glandular mass. In *M. intermedius* (fig. 3) the surface is seen to be mottled, owing to the presence of small patches of brown pigment.

Diploptrema fragilis (Pl. 15. fig. 22).—Here the gland-mass takes up the ventral surface of segments 16 to 20 or 21. It is divided up transversely by the septa which traverse it. In segment 18 the spermiducal duct runs down alongside this accessory gland-mass to open on the surface. In microscopic structure the gland-mass is very different from that in *Megascolides intermedius*. It is composed of a number of groups, a central one on which rests the nerve-cord, and two others on either side of this (*cf.* fig.). Each contains a central cavity which is lined by a single row of very granular cells varying somewhat in size, each with a nucleus. The cavity of the central group is somewhat irregular, while its floor is formed by the layer of longitudinal muscles on which are situated gland-cells. Each of the lateral groups has a definite opening to the exterior through the

body-wall (fig. 22, *a'*), but no opening could be seen in relation to the central group. It is probable, however, that this opens by means of a communication with the duct leading from the inner of each set of lateral groups. Each group is surrounded by a distinct layer containing muscle-fibres. This doubtless assists the propulsion of the secretion outwards. Between each of the two lateral groups on each side and between them and the central group, in the region of the spermiducal-duct opening, is a muscular sac (*s.s.*) containing a large curved but smooth penial seta (*s'*). There are thus two of these on each side, and the gland-groups open, not around the opening of the spermiducal duct, but around the penial setæ. This will be clear on a reference to the figure.

(2) Glands embedded in the body-wall, *e. g.* *Megascolex dorsalis* and *Digaster excavata*. In *M. dorsalis* (Pl. 15. fig. 23) there are two completely different sets of glands separated by the spermiducal duct. The first and upper of these (*a.g.*'), which lies to the outer side of the spermiducal duct, is composed of a number of alveoli. Each alveolus contains a central cavity surrounded by large finely granular gland-cells, each with a nucleus pushed to its outer edge. The alveoli are separated from each other by a number of connective-tissue septa. No connection could be traced between these and the gland-duct, though from their position it is probable that they do, at times, open into the spermiducal duct. The second set are those (*a.g.*) to be found on the inner side of the gland-duct. They are much lower down in the papilla. The cells of these groups are much smaller and clearer, though arranged as before around a central space. Each group opens on the surface not by means of a single duct, but by a number of fine ducts from the gland-cells forming the group. These run down and open to the surface between the columnar cells of the epidermis. It is the latter set only which are found in *Digaster excavata*. In this form the groups are more numerous, but more scattered and looser in structure. The groups of unicellular ducts, which are longer than in *Megascolex dorsalis*, are to be seen very clearly opening on the surface. One or two groups open into the spermiducal duct, close by the opening of the setæ into the latter.

Summary.

It will be seen from the above description that there is, in these species, a continuous series of forms of increasing complexity in internal structure. Commencing with the tubular forms, we have first those in which the gland-cells open into the lumen between the columnar cells of the lining (Pl. 14. fig. 16). There is here obviously a very close resemblance in structure to the clitellum or to the special accessory gland in *Megascolides intermedius* and *M. attenuatus*, if we neglect the occurrence of the muscle-layers there. Next we have those forms in which perhaps, on account of the increase in cornification of the lining epithelium, the gland-cells open into the lumen in groups (Pl. 15. fig. 17). The next stage is seen in such a form as *Digaster excavata*, where the lumen gives out a single series of branches, each of which bears at its end a group of gland-cells, which is thus situated at about half the thickness of the gland-wall. Here, however, the columnar lining of the main duct is not continued up these branches (cf. *Digaster excavata*).

Further complication is met with in such forms as *Megascolides illawarræ* and *Megascoplex dorsalis*, where the main duct all along its length branches considerably more than in *Digaster excavata*, and here to a great extent the branches are lined by cubical cells continuous with the columnar lining of the main duct (Pl. 15. fig. 24); but here also there is no cell-lining to the fine terminations of the branches. From these we pass to such highly complex forms as, for example, *Megascoplex tasmanica*, *M. Frenchi*, in which the main duct breaks up immediately it enters the gland, so that there is no central tube in these lobate forms (Pl. 15. figs. 19 & 20). Corresponding with this, the branching is still further increased, and as a result the lobules become more closely compacted together and fill up the entire interior of the gland. Consequent on this increase in branching, the groups are much more numerous and are pushed out towards the periphery, so that the mass of the gland is made up of these groups, the cells in which become more closely pressed together and their ducts much shortened. The blood-vessels which originally ran along the surface of the gland, or just outside the lining of the duct, have become much branched corresponding with the branching of the duct, and serve very often, with the small

amount of connective-tissue in which they run, to separate lobule from lobule, at the same time sending branches into them between the cells, to which they supply materials for secretion.

The result of this investigation into the structure of the spermiducal glands of an entirely different series of species from those studied by Beddard, clearly corroborates the statement that the more complicated lobate forms are derived in a comparatively simple way from the tubular.

Acanthodrilus sydneyensis, however, differing as it does so markedly from the *Acanthodrilidæ* generally, cannot be referred to the consecutive series at all.

Conclusions.

The following are the more important conclusions arising out of this paper:—

1. That for the glands in question there is a correspondence between internal structure and external form.
2. That there exists a complete series of conditions connecting the simplest tubular form with the most complex lobular.
3. That a cell-lining is absent from the finest terminations of the duct.
4. That the structure of the accessory glands in *Diplostrema fragilis* is peculiar, and that of the spermiducal gland in *Acanthodrilus sydneyensis* unique.

EXPLANATION OF THE PLATES.

Reference Letters.

<i>a.g.</i> , accessory glands.	<i>l.m.</i> , longitudinal muscle-band.
<i>a.g.</i> ', upper accessory glands.	<i>ll.</i> , lacuna in centre of lobule.
<i>b.v.</i> , blood-vessel.	<i>m.b.</i> , muscular bulbus.
<i>c.e.</i> , columnar epithelium.	<i>n.c.</i> , nerve-cord.
<i>c.l.</i> , cuticular layer.	<i>p.</i> , peritoneum.
<i>c.m.</i> , circular muscle-layer of body-wall.	<i>r.</i> , ciliated rosette.
<i>c.m.</i> ', circular muscle-layer of gland-duct.	<i>s.</i> , penial seta.
<i>c.t.</i> , connective-tissue.	<i>s.s.</i> , setal sac.
<i>g.c.</i> , gland-cells.	<i>s.r.</i> , sperm-reservoir.
<i>g.c.</i> ', special club-shaped gland-cells.	<i>sp.d.</i> , spermiducal duct.
<i>g.c.</i> '', duct of gland-cell.	<i>sp.d.</i> ', fine branches of spermiducal duct.
<i>l.m.</i> , longitudinal muscle-layer.	<i>sp.g.</i> , spermiducal gland.
	<i>v.d.</i> , vas deferens.

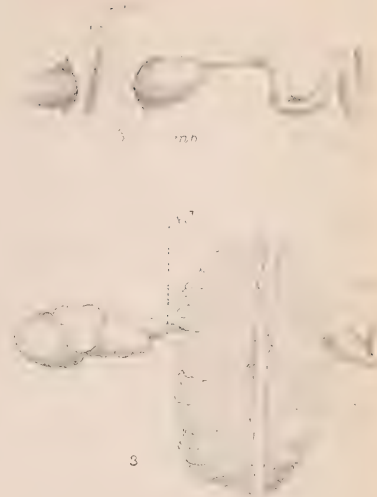
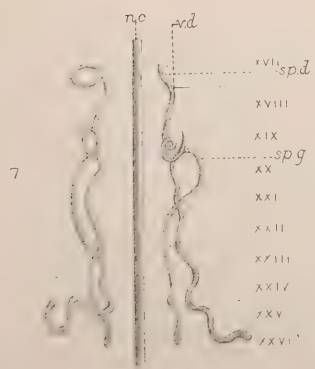
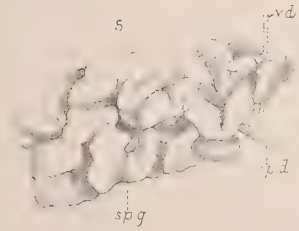
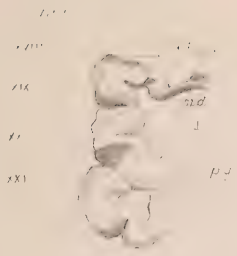
The outlines of all the figures have been drawn beneath the camera lucida, and on pl. 14 the position of the vas deferens is in all cases indicated by dotted lines.

PLATE 14.

- Fig. 1. Spermiducal gland on left side of *Diporochæta Bakeri*, showing spermiducal duct and two setal sacs. $\times 6$.
2. *Fletcherodrilus unicus*. Spermiducal gland of right side. The muscular bulbus (*m.b.*) is seen on each side to run under the ventral longitudinal muscle-band (*l.m.*) which supports the nerve-cord (*n.c.*). $\times 6$.
3. *Megascolides intermedius*. The spermiducal glands lie in segment 18, transversely to the body. On the ventral surface is seen the mass of unicellular glands, the surface being mottled with patches of pigment. The nerve-cord runs above this. $\times 6$.
4. *Megascolides victoriæ*. Spermiducal gland of right side lying in segments 18 to 29. The duct is much coiled. $\times 6$.
5. *Megascolides roseus*. Spermiducal gland of left side. Gland very much coiled. $\times 6$.
6. *Diplorema fragilis*. Spermiducal glands and ventral accessory glands. $\times 18$.
7. *Acanthodrilus sydneyensis*. Two pairs of spermiducal glands. The position and opening of the vas deferens on segment 18 is shown by a dotted line.
8. *Megascolex Frenchi*. Lobate spermiducal gland of right side, in segments 18 and 19. The markings on the surface of the gland may be clearly seen. $\times 6$.
9. *Megascolex Dendyi*. Spermiducal gland of right side. Lobate in segments 18 and 19, with a curved duct in segment 18. $\times 6$.
10. *Megascolex dorsalis*. Spermiducal gland of left side. Surface showing irregular markings. Duct very short. $\times 6$.
11. *Digaster queenslandica*. Gland of right side. Surface-markings slightly visible. No duct to be seen from above. $\times 6$.
12. *Digaster queenslandica*. Spermiducal gland of another individual. Tubular in appearance. No duct visible. $\times 12$.
13. *Digaster armifera*. Trilobed gland of right side with setal sacs and muscles belonging to them, attached to the terminal part of the gland-duct. $\times 6$.
14. *Megascolex Fielderi*. Bilobed gland of left side with lobular surface-markings. Duct curved and entering muscular bulbus. $\times 6$.
15. *Megascolex intermedius*. Portion of section showing sperm-reservoir of right side with its division into two parts, the lower containing the sperm-rosettes, and developing sperm in both. The vas deferens from the previous segment may also be seen, and the nerve-cord in position. Zeiss A.A. oc. (2).
16. *Megascolides insularis*. Transverse section of spermiducal gland showing ordinary gland-cells, special club-shaped cells, and columnar lining. The whole enclosed in peritoneum. Zeiss D. oc. (2).

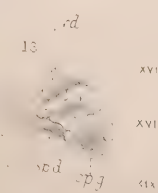
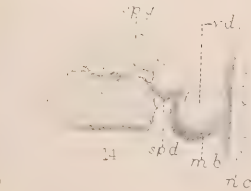
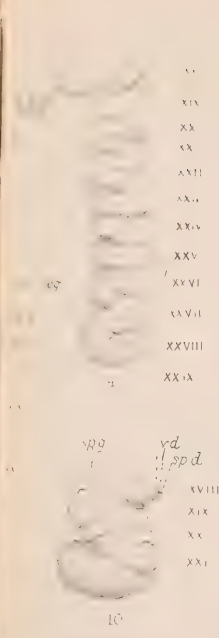
PLATE 15.

- Fig. 17. *Megascolides intermedius*. Transverse section through gland-wall, showing groups of gland-cells. The outlines of the columnar cells lining the duct are not visible. The nuclei are clearly seen, as also

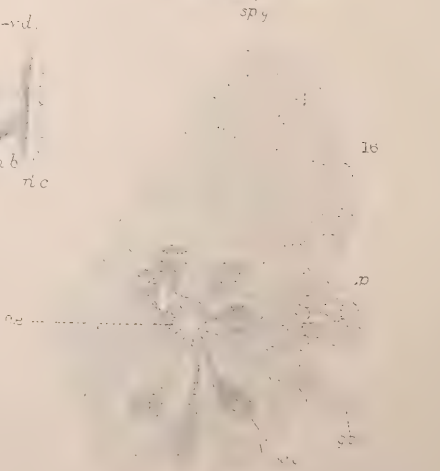
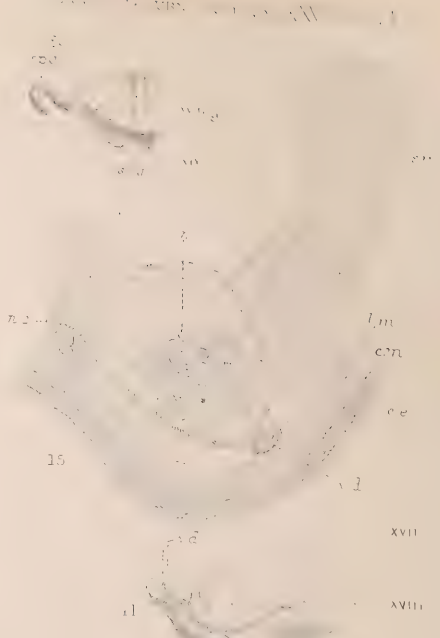


SPERMIDON

C. Laves del
A. B. Hammond lit.

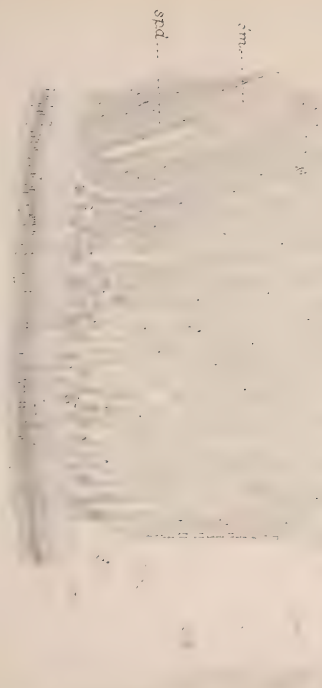


EARTHWORMS



West, Newman imp

U Sweet del
A R Hammond del



spd

sim

18

SEEDS

LEAVES



18b

19

19

g.c.

b.v.

Wesg, Newman imp

the horny layer next the lumen. Two small blood-vessels are seen running in from the surface. Zeiss D. oc. (2).

- Fig. 18 a. *Acanthodrilus sydneyensis*. Transverse section through duct of gland showing nuclei of columnar lining and the circular muscle-layer.
- 18 b. *Acanthodrilus sydneyensis*. Transverse section through the intermediate part of gland showing nuclei of columnar cells surrounded by short granular cells.
- 18 c. *Acanthodrilus sydneyensis*. Oblique section through terminal glandular part of gland. A blood-vessel is seen running up one side. The irregular gland-cells are shown; the relative depth to which they are stained with methylen-blue is shown by the shading. Zeiss D. oc. (2).
19. *Digaster brunneus*. Section across lobate gland showing the granular gland-cells and the apparently empty cells all with their ducts opening into a very small central space without any lining membrane. Around the lobule are a number of blood-vessels separating it from its neighbours. Zeiss E. oc. (2).
20. *Megascolex tasmanica*. Section across lobule in gland showing the gland-cells opening into a much larger lacuna, which is connected with one of the five terminations of the gland-duct by means of a branch with a single layer of much flattened epithelium cells. The cut ends of some of the glandular cell-ducts are seen in the lacuna. No blood-vessels were visible, and are probably present in the form of sinuses. Zeiss E. oc. (2).
21. *Megascolides intermedius*. Portion of transverse section through region of the spermiducal gland showing portion of wall of spermiducal duct cut through, and the mass of unicellular glands occupying the ventral surface here, with their ducts opening to the surface. The position of the nerve-cord is shown and the muscular layers of the body-wall. Zeiss C. oc. (2).
22. *Diploptrema fragilis*. Portion of transverse section showing the relations of the spermiducal duct, accessory glands, setæ and setal sacs, and nerve-cord. The vas deferens has opened two sections anterior to this, while the spermiducal gland opens two or three posterior to this. The opening of one group of gland-cells is seen cut through at a'. Zeiss A. oc. (2).
23. *Megascolex dorsalis*. Transverse section of the accessory glands (a.g. and a.'g.') surrounding the opening of the spermiducal gland which is seen cut through obliquely. The groups of unicellular ducts are clearly seen in the lower portion of the section. Zeiss C. oc. (2).
24. *Cryptodrilus illawarræ*. Portion of transverse section showing the lower part of the gland, the gland-duct, vas deferens, and the two setæ in their sacs. Zeiss A. oc. (2).